Yield and Yield Stability of Four Population Types of Grain Sorghum in a Semi-Arid Area of Kenya

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ABSTRACT

Sorghum [*Sorghum bicolor* (L.) Moench] is widely grown in semi-arid tropics where local farmers depend on the adaptability of their rainfed crops to unpredictable drought and other stress factors. To investigate the effects of heterozygosity and heterogeneity on the adaptability of grain sorghum, two sets of material, each containing 12 parent lines, six single-cross hybrids, six two-component blends of parent lines, and six two-component hybrid blends were grown in eight macro-environments in the semi-arid Makueni District of Kenya, during 1991 through 1993. Environmental means for grain yield ranged from 584 to 47 g m^{-2}. In all environments, hybrids outyielded their parent lines, with a mean relative hybrid superiority of 54%. Blending effects were non-significant. Combined analyses of variance were computed with logarithmically transformed data. Entry × environment interaction effects were more important than genetic effects. Lines in pure stand contributed most to the total entry × environment interaction variance. Wide ranges were found within all four groups for stability parameters derived from regression analysis. On average, hybrids in pure stand had most favorable values. Pattern analysis (classification and ordination techniques) was applied to the environment-standardized matrix of entry means from the individual environments. A one-way classification clearly distinguished homozygous from heterozygous entries. Heterogeneous entries were not consistently grouped together. Performance plots for different entry groups showed various patterns of adaptation and illustrated the superiority of heterozygous entries. The biplot from ordination underlined the importance of entry × type-of-drought-stress interaction. Principal Components 1 and 2 were highly correlated with entries' mean yield and regression coefficient, respectively. Breeding heterozygous cultivars could contribute to increased grain yields and improved yielding stability of sorghum in the target area of Kenya.

SORGHUM IS AN IMPORTANT COMPONENT in traditional farming systems in the semi-arid tropics of Africa and Asia, with mean grain yields of 863 and 1157 kg ha^{-1}, respectively (FAO, 1999). Low soil fertility, poor stand establishment, and highly variable drought stress are major production constraints in these areas. The local farmers usually do not have access to irrigation facilities or fertilizer stocks and rely totally on the stress resistance and yield stability of their rainfed crop cultivars.

Yielding stability in unpredictably variable environments can be due to individual and/or populational buffering (Allard and Bradshaw, 1964). Initially, the two mechanisms were defined by Lerner (1954) as developmental and genetic homeostasis. Individual buffering may be favored by heterozygosity, and populational buffering by heterogeneity in as much as the different genotypes present in the population are specifically adapted to different environmental conditions (Bradshaw, 1965; Reich and Atkins, 1970; Schnell and Becker, 1986). A concomitant question plant breeders are facing is, what type of genetic structure (i.e., degree of heterozygosity and heterogeneity) is most desirable—or necessary—to obtain improved, stable cultivars. Sorghum, because of the availability of nuclear and cytoplasmic-genic male sterility, offers a wide range of possible genetic structures to the breeder, including homozygous lines, homogeneous or heterogeneous hybrids, as well as homo- or heterozygous, heterogeneous populations or synthetic cultivars.

Estimates of average midparent heterosis for grain yield in sorghum range from 13 to 88%. Lower values were usually obtained with crosses of adapted parent lines (Kambal and Webster, 1966; Kirby and Atkins, 1968; Reich and Atkins, 1970; Liang et al., 1972; Patanothai and Atkins, 1974), while high estimates were most often reported from studies which involved exotic germplasm (Niehaus and Pickett, 1966; Jowett, 1972; Laosuwan and Atkins, 1977), or which were conducted under environmental stress conditions (Jowett, 1972; Kapran et al., 1997).

Five studies were found to deal with genotype mixtures in sorghum. In a trial over 5 yr at one moderate to high-yielding location in Kansas, Ross (1965) obtained 1% superiority of hybrid blends over the mean of their pure stands. The hybrids involved in this study differed in days to anthesis by maximally 11 d. Reich and Atkins (1970) reported a mean blending effect for grain yield of 2%, averaged over homozygous and heterozygous entries and nine moderate to high-yielding environments in Iowa. Results from an experiment grown at four locations in Ghana with environmental means for grain yield between 254 and 2869 kg ha^{-1} indicated a slightly larger, but still non-significant yield advantage of two- to five-component blends of local cultivars over the individual pure stands (Mercer-Quarshie, 1979). Marshall and Allard (1974) who studied the performance of lines in pure stand and two-, four-, six-, twelve-, twenty-, fifty-, and eighty-component mixtures in nine non-stress site–season combinations in California stated that favorable blending effects were seldom of sufficient magnitude to offset the burden imposed on heterogeneous populations by the lower yielding genotypes. Yet, Bebawi and Abdelaziz (1983) reported a 25% superiority of two-component blends of cultivars differing largely in their maturity dates over the mean of their pure stands in a study conducted at one location over 2 yr with differing drought stress intensity in Sudan.

Regarding stability of grain yield, Reich and Atkins (1970) reported hybrid blends to be the most productive

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Table 1. Designations of the hybrids, parent lines, and standards evaluated in the present study; abbreviated designations in brackets.

Set 1				Set 2			
Hybrid	Female parent	Male parent	Standards	Hybrids	Female parent	Male parent	Standards
SDSH 409 (H1)	Ma 6 (B1)	R 8602 (R1)	Makueni (Mak)	SDSH 300 (H1′)	ICSA 20 (B1′)	SDS 170 (R1′)	Makueni (Mak)
SDSH 19 (H2)	ATX623 (B2)	SDS 3219 (R2)	Seredo (Ser)	SDSH 48 (H2′)	ICSA 12 (B2′)	SDS 6013 (R2′)	Seredo (Ser)
ICSH 110 (H3)	ICSA 296 (B3)	ICSR 33 (R3)	ICSH 88058 (HSt1)	SDSH 339 (H3′)	ATX 631 (B3′)	A 6352 (R3′)	ICSH 88058 (HStl′)
SDSH 315 (H4)	ICSA 21 (B4)	R 8609 (R4)	SDSH 148 (HSt2)	SDSH 343 (H4′)	SDS 2690 (B4′)	A 150 (R4′)	SDSH 382 (HSt2′)
SDSH 215 (H5)	SPL 23 A (B5)	MR 855 (R5)	ICSH 807 (HSt3)	SDSH 4 (H5′)	D2 A (B5′)	SDS 3880 (R5′)	BTx 629 (BSt3′)
ICSH 205 (H6)	ICSA 51 (B6)	ICSR 152 (R6)	ICSB 32 (BSt4)	SDSH 398 (H6′)	A 8607 (B6′)	ZAM 1518 (R6′)	SDS 2302 (RSt4′)

and stable population type. Jowett (1972) and Patano-thai and Atkins (1974) compared heterogeneous three-way crosses with homogeneous single crosses at eight and nine environments in Uganda and Iowa, respectively. Considerable variation was found among the individual hybrids for stability parameters, suggesting that stability of performance may be attainable with both hybrid types. Mercer-Quarshie (1979) reported a trend of increasing stability with increasing complexity of the mixtures in Ghana.

Overall, only limited knowledge is available about the effects of heterozygosity, heterogeneity, and their interaction on the performance of sorghum grown under unpredictable stress conditions. Our experiment was, therefore, designed to examine yield level and stability, and patterns of genotype × drought stress interactions in a genetically balanced system of sorghum entries differing in heterozygosity, heterogeneity, or both in a semi-arid area of Kenya.

MATERIALS AND METHODS

The basic material consisted of 12 unrelated single-cross hybrids and their respective 24 homozygous parent lines ($>F_9$ inbreeding generation). These genotypes represented a random sample of actual sorghum breeding germplasm from SADC/ICRISAT (Southern African Development Community/ International Crops Research Institute for the Semi-Arid Tropics) in Zimbabwe. To reduce the size of individual experiments and herewith the experimental error due to natural heterogeneity of the experimental fields, the materials were randomly divided into two sets (Table 1). Within each set, the following four groups of entry with alternate types of genetic structure were formed, analogous to the experiments of Reich and Atkins (1970) with sorghum and Schnell and Becker (1986) with maize (*Zea mays* L.):

1. Homogeneous entries of homozygous plants: six female lines (B1, ..., B6) and six male lines (R1, ..., R6), using maintainer versions (B lines) of the cytoplasmic-genic male sterile lines;
2. Homogeneous entries of heterozygous plants: six single-cross hybrids among the above 12 parent lines (H1, ..., H6);
3. Heterogeneous entries of homozygous plants: six two-component blends of the parent lines according to the parentage of the hybrids (Lm1, ..., Lm6, corresponding to blends of the lines B1+R1, B2+R2, ..., B6+R6, respectively);
4. Heterogeneous entries of heterozygous plants: six two-component blends of hybrids such, that each hybrid was included in two mixtures (Hm12, Hm34, Hm56, Hm14, Hm25, Hm36, corresponding to blends of the hybrids H1+H2, H3+H4, ..., H3+H6, respectively).

Within each set, the arrangement is genetically balanced in

that all four groups of entry share the same set of nuclear genes in equal frequencies. The two sets were each planted together with six standard cultivars (Table 1) in 6 by 6 triple lattice designs side by side in the same field. The standards included the two local cultivars Makueni and Seredo which can be considered improved open-pollinated cultivars with unknown degree of heterozygosity and heterogeneity. The choice of the other standards was determined by seed availability.

The experiment was conducted during 1991 to 1993 in eight macro-environments (site–season combinations) at the semi-arid locations Kibwezi (latitude 2°17′S; longitude 38°01′E; altitude 800 m) and Kiboko (latitude 2°12′S; longitude 37°43′E; altitude 915 m; both Makueni District, Kenya; Table 2). The long-term average rainfall at Kibwezi and Kiboko amounts to 368 and 320 L m^{-2} in the Short Rains and to 239 and 195 L m^{-2} in the Long Rains, respectively (Michieka and Van der Pouw, 1977; Ekirapa and Muya, 1991). The annual rainfall at Kibwezi fluctuated from 67 to 1964 L m^{-2} in the years from 1919 to 1974.

Plots consisted of three or four rows, 3 or 4 m long with 0.8 m inter-row spacing, resulting in plot sizes between 9.6 and 12.8 m² (Table 2). The experiments were hill planted by hand and thinned to one plant per hill, aiming at a final density of 6.25 plants m^{-2}. To ensure a true 1:1 mixture in the heterogeneous entries, the components of each blend were sown alternately in the successive hills of each row. Supplementary irrigation for stand establishment was given in some environments. The total amount of water received by the individual experiments ranged from 150 to 1078 L m^{-2}. Experiments in the Long Rains 1993 relied on irrigation and residual soil moisture from the previous, outstandingly abundant Short Rains. Soil types were Chromic Luvisol at Kibwezi, and Luvisol at Kiboko. Fertilizers were applied at Kibwezi A in the Short Rains 1991/92 (100 kg N, 50 kg P$_2$O$_5$, 50 kg K$_2$O ha^{-1} before planting) and at Kiboko in the Long Rains 1993 (50 kg N ha^{-1}, top-dressed). Plants were chemically protected against insects when necessary. Birds were scared away from flowering to harvest time. Weeding was done by hand. Several traits were assessed but only data of grain yield [g m^{-2}, at 9.5–10% grain moisture, estimated on the basis of the whole three or four-row plot] is reported here. Grain yields were linearly corrected in case of bird or squirrel damage which was visually estimated. No adjustment was undertaken for missing plants. Observations on rainfall distribution, leaf rolling, leaf firing, and days to anthesis of sorghum were used to determine the type of drought stress in individual environments.

The computer program PLABSTAT (Utz, 1993) was used for initial statistical analyses. Entries and environments were considered as factors with random effects while the effects of heterozygosity and heterogeneity were regarded as fixed. In a first step, data of each set were analyzed according to the lattice design. Drought intensities were computed relative to the mean of the two highest yielding environments as described by Fischer and Maurer (1978). Repeatabilities (= heritabilities on plot basis) were calculated as outlined by Fehr

Table 2. Site–season combinations, rows per plot and plot sizes employed, respective amount of water received, kind of drought stress, and allocated environmental codes.

Season† and year	Site‡	Rows plot⁻¹	Plot size	Amount§ of water			Mean grain yield	Kind of drought stress¶	Code
				Rain	Irrigation	Total			
			m^2		$L\ m^{-2}$		$g\ m^{-2}$		
SR 1991/92	Kibwezi A	3	9.6	375	55	430	584	Non-stress	N1
	Kibwezi B	3	9.6	373	0	373	297	Moderate terminal	D1T
LR 1992	Kibwezi A	4	9.6	219	40	259	47	Extreme (preflowering and terminal)	D6E
	Kibwezi C	4	9.6	275	0	275	154	Moderate terminal	D5T
SR 1992/93	Kibwezi A	4	12.8	1058	20	1078	537	Non-stress	N2
	Kiboko	4	12.8	557	40	597	284	Preflowering, followed by rains	D2P
LR 1993	Kibwezi A	4	12.8	R + 23	150	R + 173	222	Moderate terminal	D3T
	Kiboko	4	12.8	R + 1	151	R + 151	221	Moderate terminal	D4T

† Two Rainy Seasons per year in Kenya: Short Rains (SR) and Long Rains (LR).
‡ A = Irrigation Project, B = Goat Research Station, both University of Nairobi; C = Local farm.
§ R = Residual moisture from previous Short Rains.
¶ Based on observations on rain distribution and leaf rolling or leaf firing of sorghum in the individual experiments.

(1987). Heterogeneity of error variances was tested with Bartlett's Test (Snedecor and Cochran, 1980). Combined analyses of variance across environments were computed with logarithmically transformed data $\{y = \ln[(x/10)+1]\}$ since genetic and environmental effects were related in a multiplicative manner, as indicated by Tukey's (1949) test for non-additivity. Numerical stability parameters were estimated according to Eberhart and Russell (1966) with the logarithmically transformed data. A low regression coefficient, combined with a low deviation mean square and a relatively high grain yield in the low-yielding environments was considered advantageous. Coefficients of phenotypic and genotypic correlation were calculated as described by Mode and Robinson (1959).

Pattern analysis by the software package GEBEI (Watson et al., 1996) was applied to the environment-standardized (Fox and Rosielle, 1982) matrix of the lattice-adjusted entry means from the individual environments. The environment standardization is designed to group environments that are most similar in the way they cause genotypes to be ranked (Fox and Rosielle, 1982). An agglomerative hierarchical procedure with an incremental sum of squares grouping strategy known as Ward's method (Ward, 1963) was employed for the purpose of classification. The squared Euclidean distance was used as dissimilarity measure required in Ward's method. A one-way classification of the entries was chosen, maintaining all eight macro-environments as separate. The number of entry groups was determined considering the percentage of the sums of squares retained in the reduced entry × environment matrix. Performance plots of different entry groups were used to illustrate various adaptation patterns of the entries. The biplot derived from ordination served to assess relations among entries, among environments, and between entries and environments (Kempton, 1984). Entries close to the origin are average in their performance across all environments. Entries or environments that are close to each other tend to be similar. Entries distributed in the increasing direction of an environment vector are positively associated with that environment, while those distributed in the opposite direction are negatively associated. A line drawn perpendicular from a particular entry to an environment vector indicates its relative performance in that environment, i.e., for the same environment vector, a better genotype would project an intersection point that is farther along in the positive direction of the environment vector. Small angles between two environment vectors indicate strong positive associations, i.e., high similarity between these two environments; 90° angles indicate no association; and angles greater than 90° indicate negative associations.

RESULTS

Growing conditions during the experimental period were highly variable and were comprised of two non-stress and six stress environments (including preflowering, terminal, and extreme drought). Correspondingly, environmental means for grain yield ranged from 584 to 47 g m⁻² (Table 2). In the following, the two non-stress environments will be named N1 and N2, and the six stress environments D1T, D2P, D3T, D4T, D5T, and D6E, respectively. The D-codes relate to increasing drought intensities and decreasing yield levels; T, P, and E denote presence of terminal, preflowering, and extreme (preflowering and terminal) drought stress, respectively.

Heterozygous entries significantly outyielded homozygous entries in all environments (Fig. 1), with a mean relative hybrid superiority of 54%, averaged over both
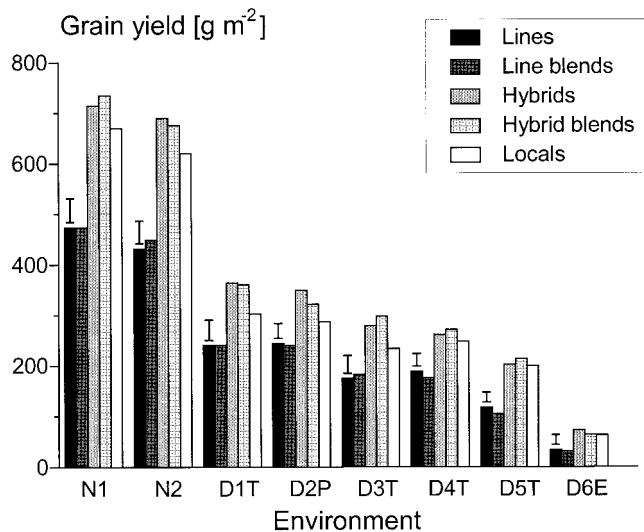

Fig. 1. Means of the four groups of entry and the two local cultivars for grain yield in two non-stress (N1, N2) and six stress environments (D1T, D2P, D3T, D4T, D5T, D6E, with the numbers denoting increasing drought intensity, and T, P, and E terminal, preflowering, and extreme drought stress, respectively) in a semi-arid area of Kenya, averaged over the two sets of material. Vertical bars indicate least significant differences ($P = 0.05$) among the entry types.

Table 3. Estimated repeatabilities (underlined on diagonal) in and coefficients of correlation among environments for grain yield, pooled over the two sets of material including all entries and standards.

	Environment and kind of drought stress							
	Non-stress		Preflow.	Terminal				Extreme
Environment	N1	N2	D2T	D1T	D3T	D4T	D5T	D6E
N1	<u>93.5</u>							
N2	0.85**	<u>96.1</u>						
D2P	0.65**	0.79**	<u>91.9</u>					
D1T	0.82**	0.76**	0.60**	<u>77.8</u>				
D3T	0.64**	0.73**	0.42**	0.65**	<u>87.4</u>			
D4T	0.68**	0.74**	0.52**	0.67**	0.67**	<u>85.9</u>		
D5T	0.75**	0.73**	0.49**	0.73**	0.66**	0.63**	<u>89.6</u>	
D6E	0.39**	0.39**	0.20	0.38**	0.44**	0.39**	0.59**	<u>83.8</u>

** Significant at the 0.01 probability level.

levels of heterogeneity. The latter value ranged from 36 to 107% across the individual environments. The highest estimates of hybrid superiority were obtained in the two lowest yielding environments. Differences between blends and pure stands were small and inconsistent across environments for both lines and hybrids. Averaged over the eight environments, two sets of material, and both levels of heterozygosity, the mean blending effect was not significantly different from zero. The same was true for the interactions of heterogeneity with heterozygosity and with environments, and for the respective threefold interaction. Hybrids outyielded the local cultivars Makueni and Seredo by 10 and 14%, respectively.

Strong correlations occurred between the environments without stress (N1, N2) and those with preflowering (D2P) or moderate terminal drought stress (D1T, D3T-D5T, Table 3). Among the latter environments the relationships were somewhat weaker but still highly significant. Only weak or non-significant relationships existed between the extreme stress environment (D6E) and most other environments. These weak associations were not due to a reduced differentiation among entries, since repeatabilities for grain yield were moderate to high in each environment. The highest estimates of repeatability were obtained in the two non-stress environments. The lowest value appeared in the third highest yielding environment D1T.

The logarithmic transformation strongly reduced non-additivity, but error variances still remained heterogeneous so that the F-tests in the combined analyses of variance were only approximate (Cochran and Cox, 1957). Estimated genetic variances were significant only among lines (Table 4). Entry × environment interaction

variances were more important than genetic variances in all four entry groups. Lines contributed more than hybrids to the total entry × environment interaction variance. Genotypic heterogeneity reduced entry × environment interaction at the homozygous but not at the heterozygous level.

Regressions of entry means in individual environments on the respective environmental means for grain yield differed significantly ($P \leq 0.01$) among the entries. The heterogeneity of regressions explained 33 and 41% of the total entry × environment interaction variance in the two sets of material. On average, homozygous entries had a slightly higher regression coefficient than heterozygous entries (Table 4). However, the ranges of the regression coefficients were rather wide, being largest among lines and smallest among line blends. Ranges of the deviation mean squares were large as well. On average, lines had the largest deviation mean square, whereas differences between the other three groups were negligible. The local cultivars had regression coefficients below unity ($b = 0.96$ and 0.86 for Makueni and Seredo, respectively, averaged across the two sets of material). Makueni proved to be very stable as judged from its deviation mean square ($s_d^2 = 12$) while Seredo ($s_d^2 = 45$) ranked close to the mean of the lines. There was no association between the entry mean and the regression coefficient or deviation mean square for grain yield.

The dendrogram for the eight environments derived from pattern analysis clearly separated the extreme stress environment D6E from all other environments in both sets of material (Fig. 2). The non-stress environments N1 and N2 grouped closely together in both sets of material, whereas the divergence among the drought

Table 4. Estimated genotypic (G) and entry × environment interaction (G × E) variances, and regression coefficients and deviation mean squares of four groups of genetic entries for grain yield (logarithmic scale), based on eight (two non-stress and six stress) environments and pooled over the two sets of material.

	Variance components ± standard error		Regression coefficient†		Deviation mean square‡	
Entry group	G	G × E	Mean	Range	Mean	Range
Lines	19.5** ± 9.2	77.5** ± 10.9	1.02	0.6–1.5	49	4–217
Line blends	0.5 ± 2.5	24.9* ± 7.2	1.07	0.9–1.3	35	14–57
Hybrids	3.5 ± 4.1	30.8** ± 8.2	0.94	0.7–1.3	28	5–58
Hybrid blends	0.6 ± 3.1	34.6** ± 8.8	0.98	0.6–1.2	31	5–75

*, ** F-test significant at the 0.05 and 0.01 probability levels, respectively.
† Heterogeneity of regression coefficients and deviation mean squares highly significant in both sets of material ($P \leq 0.01$).
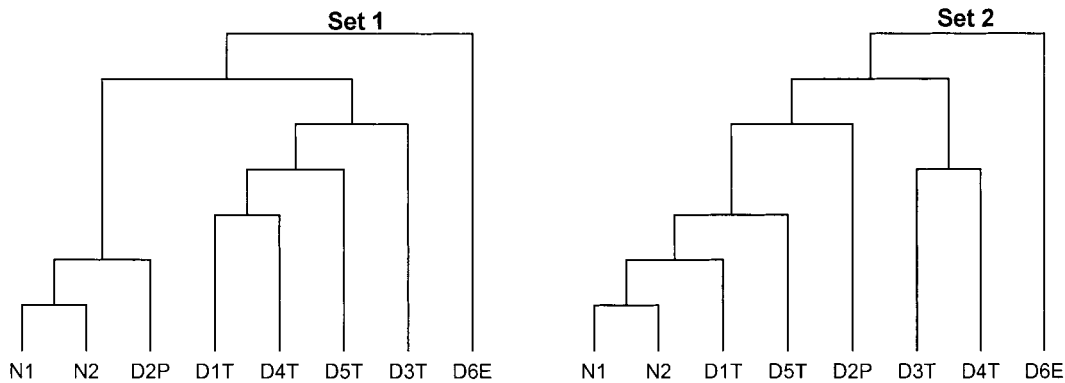‡ Estimates multiplied by 1000.

Fig. 2. Hierarchical classification of the eight environments obtained from the data of a) Set 1, and b) Set 2. Environment abbreviations as in Fig. 1.

stress environments D1T, ..., D5T did not fully correspond to the performance level for grain yield or the type of drought stress observed in these environments.

The one-way classification of the 36 entries of Set 1 and Set 2 resulted in nine and eight entry groups, respectively (Fig. 3). Ninety-five and 92.8 % of the sums of squares for differences among entries were retained in the reduced matrix in Sets 1 and 2, respectively. The percentage of retained entry × environment interaction sums of squares amounted to 54.3 and 53.6% in Sets 1 and 2, respectively. In both sets of material, the classification clearly separated homozygous (Groups G1–G4 and G1'–G4' in Sets 1 and 2, respectively) from heterozygous (G5–G9 and G5'–G8' in Sets 1 and 2, respectively) entries. The local cultivars ranked among the hybrids. Heterogeneous entries were not consistently grouped together.

Performance plots of the individual entry groups show various patterns of adaptation to the test environments (Fig. 4), and illustrate the above-average performance of heterozygous entries and local cultivars (broken lines) for both sets of material in almost all environments. Exceptions are G8' of Set 2 with sensitivity to preflowering and extreme drought, and G7' of Set 2 with below-average performance under extreme stress. Positive interactions with preflowering drought were found among both homozygous and heterozygous entry groups, i.e., for G2, G3, and G8 of Set 1, and for G2' and G7' of Set 2. Adaptation to extreme stress was indicated for G6 (Seredo) and G7 in Set 1, and for G4', G5', and G6' in Set 2. Group G1' of Set 2, consisting of six B lines, one R line and two line mixtures, appeared to be the most stable group, but at a poor performance level throughout. While G1 of Set 1 was relatively better adapted to the lower yielding environments, G9 in Set 1 and G3' in Set 2 were relatively better adapted to the higher yielding environments. The on average highest yielding entry groups were G6' of Set 2 and G7 of Set 1 (Table 5). Group G6' included the hybrids SDSH 4 and SDSH 398 in pure stand, and the hybrid mixtures SDSH 4–SDSH 398 and SDSH339–SDSH 398. Group G7 consisted of the hybrids SDSH 215 and ICSH 807, and the hybrid mixtures ICSH 110–SDSH 315 and SDSH 215–ICSH 205 (Fig. 2, Table 1). The nine–eight entry groups in Set 1–Set 2 differed significantly in their

mean days to 50% anthesis (Table 5). The on average highest yielding entry groups (G6' and G7) were among the four earliest flowering groups. Adaptation to pre-flowering drought followed by rain was associated with comparatively later flowering in the entry groups G2, G3, G2', and G7'. The extraordinary adaptation of group G4' in Set 2 to extreme drought stress was associated with escape through early flowering.

The first two principal components from ordination analysis explained 80 and 76% of the total sums of squares of the entry × environment interaction in Set 1 and Set 2, respectively. Entry values for the first principal component were strongly correlated with the mean grain yield across the eight environments (coefficient of phenotypic correlation $r = 0.99$, pooled over Set 1 and Set 2, significant at $P \leq 0.01$). The Principal Component 2 was highly correlated with the regression coefficient estimated as stability parameter according to Eberhart and Russel (1966) (coefficient of phenotypic correlation $r = -0.78$, pooled over Set 1 and Set 2, significant at $P \leq 0.01$).

The corresponding biplots (Fig. 5) showed that there was no correspondence between the discrimination among entries in the environment with solely preflowering drought versus the environment with extreme drought stress in both sets of material (i.e., 90° angle between the two respective environmental vectors). The angles between vectors of the environment with pre-flowering drought and those with terminal drought were larger than angles between non-stress and the various stress environments, indicating the presence of genotype × type-of-drought-stress interaction. The biplots from both sets of material clearly illustrate the better adaptation of heterozygous entries and local cultivars to the testing environments. Perpendicular lines drawn from homozygous entries meet most environmental vectors at negative values, reflecting the generally poor performance.

A strong, positive genotypic correlation was obtained between midparent and hybrid performance for grain yield ($r = 0.74$, pooled over Set 1 and Set 2; estimate exceeds its standard error once), whereas no significant relationship existed between the blends and the mean of the corresponding pure stands. No significant association between parents and hybrids or blends was ob-
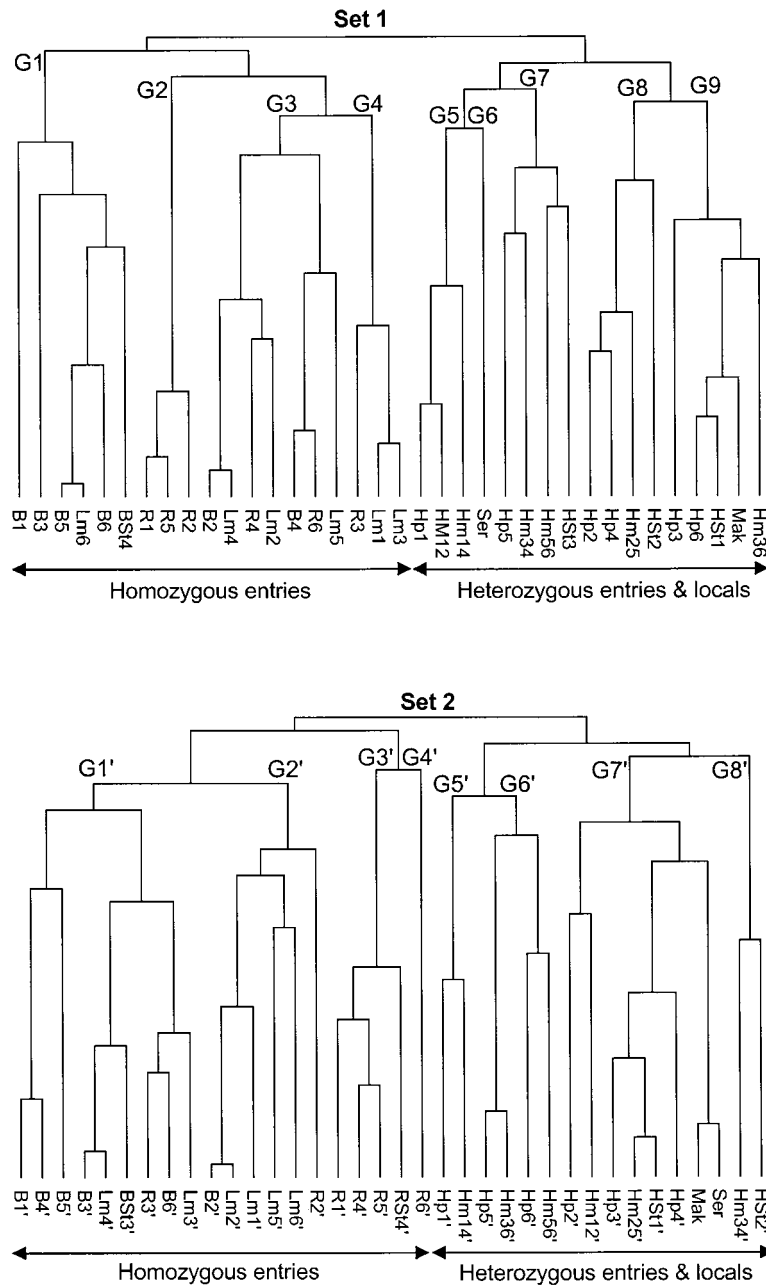
Fig. 3. Dendrograms showing hierarchical classification of 36 entries in a) Set 1 and b) Set 2, based on environment-standardized grain yield data from eight Kenyan macro-environments. Abbreviations of genotypes as in Table 1.

served for the stability parameters. Coefficients of phenotypic correlation were mostly positive but non-significant between parents, hybrids, or blends for the Principal Components 1 and 2.

DISCUSSION

The target environment of the present study is characterized by extreme variability of environmental conditions within a relatively small area. This was reflected by the huge range of environmental means for grain yield (47–584 g m^{-2}) obtained during the experimental period of only 2 yr and by the low coefficients of correlation among certain environments. Detailed long-term

agroclimatic studies, i.e., with estimates of frequencies and intensities of post planting, preflowering, and terminal drought stress in the area are not available. However, on the basis of rainfall probability estimates, Ekirapa and Muya (1991) stated that farmers in the Kibwezi area suffer from poor crops or crop failures (total rain $<\frac{1}{2}$ total potential evaporation) in four out of 10 Short Rains and in six out of 10 Long Rains, while a good crop (total rainfall $> 2/3$ total potential evaporation) may be expected in four out of 10 Short Rains and only in two out of 10 Long Rains. The probability of crop failures is even higher at Kiboko because of the lower average amount of rain. The impact of crop failures is an important aspect when defining adaptation. Though
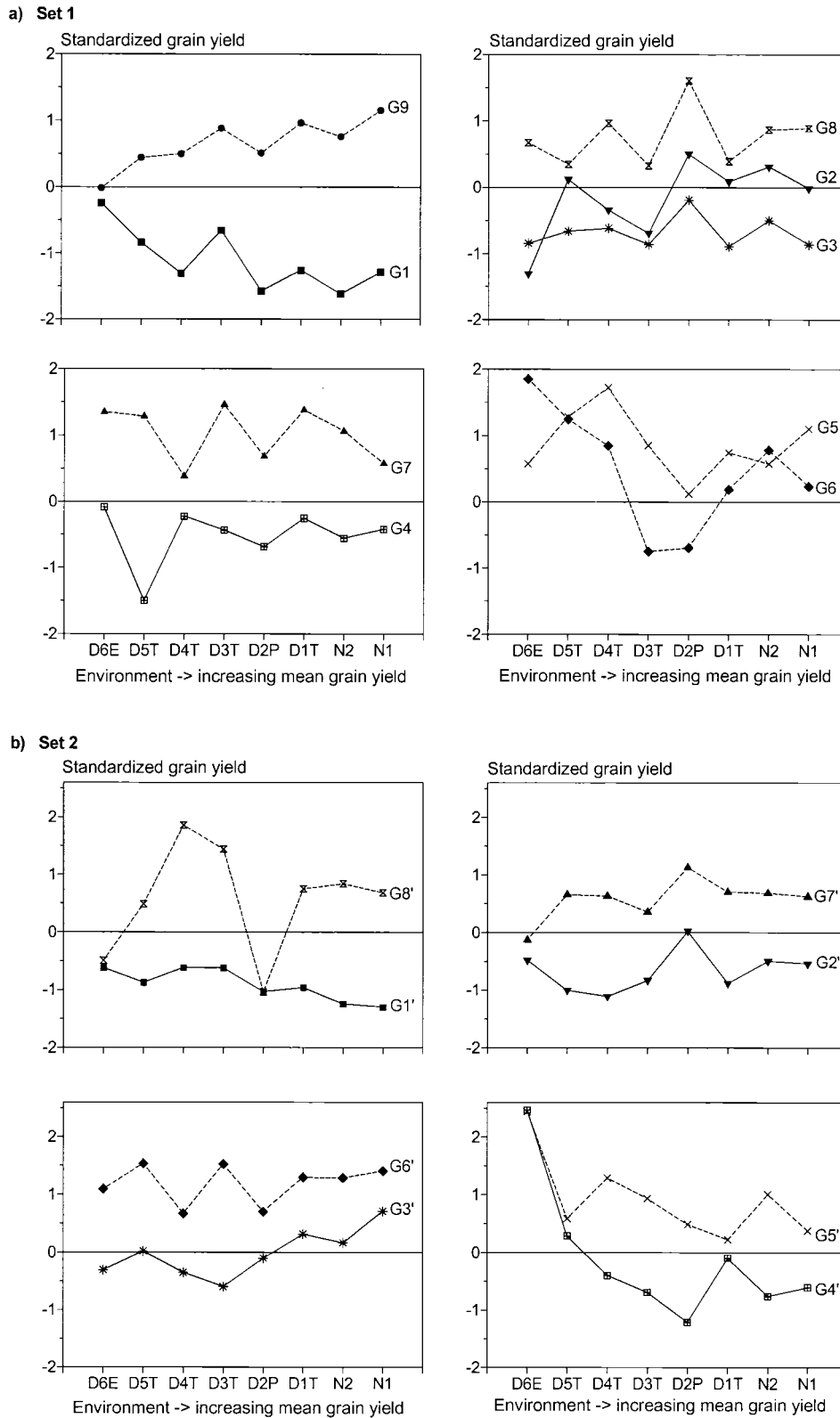
a) **Set 1**

b) **Set 2**

Fig. 4. Performance plots of entry groups a) G1, ..., G9 in Set 1 and b) G1', ..., G8' in Set 2. For group compositions see Fig. 3.

no socio-economic investigation quantifying the risk aversion of people in the Makueni district of Kenya is available, a high risk aversion of the prevailing subsistence farmers can be assumed. Therefore, cultivars are needed with specific adaptation to extreme stress condi-

tions and broad adaptation to all other, unpredictable types of environments occurring in the area.

Landraces can be considered as the outcome of an evolutionary approach to survival and performance under arid and semi-arid conditions (Ceccarelli, 1994).

Table 5. Mean grain yield (g m⁻²) of the entry groups in Set 1 and Set 2 derived from pattern analysis, averaged across the eight macro-environments.

Set	Trait†	Entry group in Set 1/Set 2
		1/1′	2/2′	3/3′	4/4′	5/5′	6/6′	7/7′	8/8′	9	LSD‡
1	GY	192	296	241	253	366	326	378	364	361	55
	AN	65	68	68	67	62	65	63	64	66	1
2	GY	208	240	303	260	351	392	342	343	–	58
	AN	69	68	66	58	64	62	66	65	–	1

† GY = grain yield; AN = days to 50% anthesis.
‡ Least significant difference for group mean differences at $P = 0.05$.

Thus, their genetic structure must bear some advantage or at least, cannot be "accidental" (Ceccarelli et al., 1991). Hayward and Breese (1993) described the genetic structure of inbred cereal landraces as "stable mixture of coadapted genotypes having different and complementary requirements for resources such as nutrients and light, and thus escaping competitive elimination". A certain degree of heterozygosity may be expected as well, depending on the individual outcrossing rates. In sorghum, outcrossing was rated at 5 to 15% in cultivated sorghum and up to 30% or more in wild relatives (Doggett, 1988).

In the present study, heterozygosity turned out to be an important prerequisite of high grain yield in sorghum grown under drought stress in the Kenyan target area. The obtained mean relative superiority of hybrids over lines for grain yield lies above the average value given for sorghum in the literature. This may be explained by a lack of adaptation of some of the female lines which resulted in a lower midparent performance but was overcome in the hybrids by the genetic contribution of the male parent. The comparatively good performance of the local cultivars Makueni and Seredo and their co-classification with hybrids indeed indicate that the "locals" were better adapted to drought stress than most parent lines. However, the higher yielding ability of the locals could as well have resulted from a certain degree of heterozygosity. In this context, it would have been useful to include a treatment of hybrid blends that had been taken to F_2 or F_3 to obtain checks that were more relevant to the local standards.

The phenomenon of heterosis is particularly important in outcrossing species [e.g., 92–252% in maize (Schnell and Becker, 1986; Melchinger and Gumber, 1998), 81–207 % in rye (*Secale cereale* L.) (Geiger and Miedaner, 1997), and least important in self-pollinating species [e.g., on average 9% in wheat (*Triticum aestivum* L.) (Melchinger and Gumber, 1998)]. Partially allogamous species were found to range between the two extremes, as shown for sorghum in this study, or observed for spring faba bean (*Vicia faba* L.) by Stelling et al. (1994). The larger relative superiority of heterozygotes over homozygotes in outcrossing species appears to be mainly due to their higher degree of dominance (Geiger, 1988) and the concomitant higher mutation load which becomes apparent during the process of inbreeding (Gallais, 1988).

The heterozygous entries were, on average, slightly more stable than the homozygous ones, but the wide ranges found within both lines and hybrids for stability parameters indicate that it should be possible to select stable entries at both levels of heterozygosity. These results agree with the findings of Reich and Atkins (1970), Majisu and Doggett (1972), and Patanothai and Atkins (1974). The effect of heterozygosity on yield stability varies among crop species, depending on their reproductive system (Léon, 1994). In outcrossing species like maize (Schnell and Becker, 1986) and rye (Wahle and Geiger, 1978), heterozygosity has a strong positive effect on yield stability. In partially allogamous species like oilseed rape (*Brassica napus* L.) (Léon, 1991), faba beans (Stelling et al., 1994), and sorghum (Reich and Atkins, 1970), heterozygosity may improve yield stability, but to a lower extent than in purely out-
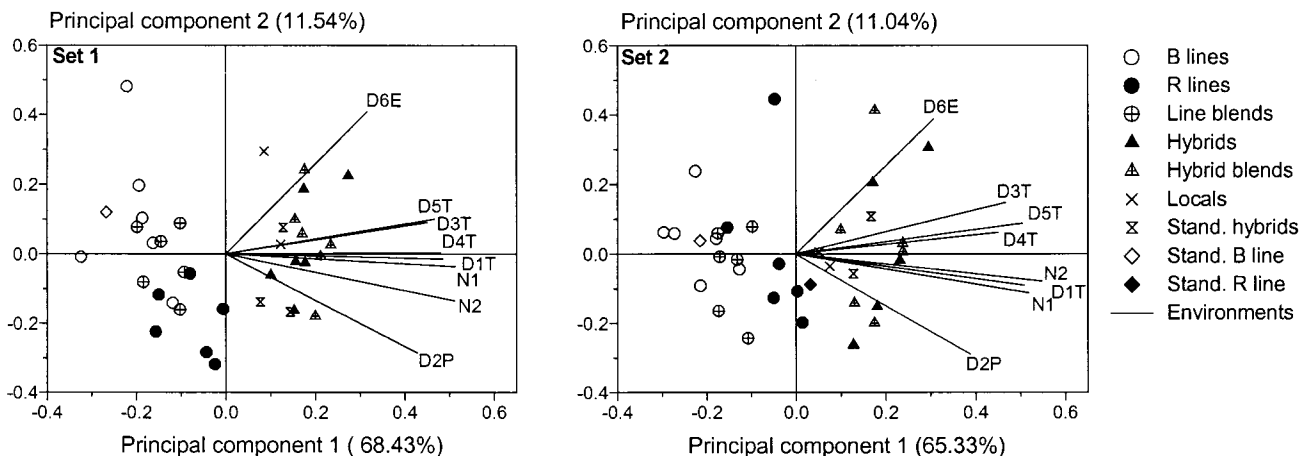

Fig. 5. Biplots for Principal Components 1 and 2 obtained from the ordination of environment-standardized grain yield data of a) Set 1 and b) Set 2. Environments are characterized by vectors drawn from the origin. For environmental abbreviations see Fig. 1.

crossing species, while in inbreeders no benefit from heterozygosity per se on yield stability has been found so far (Léon, 1994).

Blending effects were small, inconsistent, and non-significant for grain yield of both lines and hybrids. Possible reasons for the general lack of blending effects in this study may be that the tested genotypes were not selected for high performance in mixtures, and that they did not differ extremely in developmental or morphological traits. Apart from limited stemborer [*Chilo partellus* (Swinhoe), *Sesamia calamistis* Hmps.], shootfly [*Atherigona soccata* (Rondani)], charcoal rot [*Macrophomina phaseolina* (Tassi) Goid], or grain mold (*Fusarium* and *Curvularia* species) infestation in single environments, no marked diseases or pests were encountered. Therefore, potential advantages of genetic heterogeneity, caused by lower intergenotypic competition, and/or reduced spread of pests and diseases could not materialize. Reviewing results from several crop species, Allard and Hansche (1964) indicated that mean yields of mixtures hold an average advantage in the order of 3 to 5% over the means of their components. Later, Clay and Allard (1969) noted that in only 10% of all reported cases in barley (*Hordeum vulgare* L.), the superiority of mixtures was statistically significant.

Blending reduced estimated entry × environment interaction variances and deviation mean squares at the homozygous but not at the heterozygous level. Possibly, effective populational buffering requires more diverse hybrids or more complex hybrid mixtures than those evaluated in this study. Similar findings have been obtained for maize by Schnell and Becker (1986). In contrast, Reich and Atkins (1970) and Stelling et al. (1994) found the increased yield stability of hybrid blends in sorghum and faba beans, respectively, to result additively from the effects of heterozygosity and heterogeneity. Yield stability of oilseed rape was reported to profit more from heterogeneity than from heterozygosity (Léon, 1991). However, as the studies mentioned here were not conducted under drought stress, they may not be directly comparable to our results. In barley, some individual lines were shown to be as stable as local heterogeneous populations in Mediterranean, semi-arid climates, at least in the short term (Ceccarelli, 1994).

The biplot visualized large entry × environment interactions for grain yield under preflowering versus terminal and/or extreme drought stress, and extreme versus moderate or non-stress conditions. These relations were also reflected in the phenotypic correlations among the environments. Similarly, Walulu et al. (1994) reported sensitivity to terminal drought of sorghum genotypes with resistance to preflowering stress and vice versa, and Ceccarelli (1994), Ud-Din et al. (1992), and Virk and Mangat (1991) indicated low genetic correlations between grain yield under extreme stress and non-stress conditions for barley, wheat, and pearl millet [*Pennisetum americanum* (L.) Leeke].

Genetic variation for days to anthesis affected the adaptation to the different drought stress environments in the present study. The best adapted entry groups flowered relatively early, at about 62 to 63 d after planting. In another approach using the same data set, a multiple regression of grain yields under stress on yield potential and days to 50% anthesis was computed for lines and hybrids in pure stands for each stress environment (Haussmann et al., 1998). Differences in yield potential contributed to grain yield differences in all stress environments. Early anthesis was more important than yield potential for specific adaptation to extreme drought. A slight advantage of early anthesis was indicated for environments with terminal drought, while in D2P, characterized by preflowering stress followed by rains, a late onset of anthesis was slightly beneficial.

The present study was not designed to estimate heritabilities for yielding performance at different kinds and intensities of drought stress. However, the repeatabilities given in Table 3 indicate an upper limit on the genetic variability under drought versus non-stress conditions. The repeatabilities for grain yield were highest in the two non-stress environments, but lowest in the third highest yielding environment D1T. These results suggest lower heritabilities under stress relative to non-stress conditions, but do not imply a linear decline of heritabilities with increasing stress intensities. Similarly, heritability estimates were found to be slightly lower under stress conditions for grain yield in wheat (Ud-Din et al., 1992) and pearl millet (Bidinger et al., 1994), and independent from the stress intensity for grain yield of barley (Ceccarelli et al., 1987; Ceccarelli, 1994).

Large genotype × environment interaction effects within a spatially limited area point to the necessity of evaluating breeding materials under a wide range of environmental conditions to achieve broad adaptation. In weighing selection criteria when breeding in semi-arid climates, particular emphasis should be given to specific adaptation to extreme drought stress, since achieving a reliable minimum grain yield is more important to the risk-averse subsistence farmers than high yields in the rare favorable seasons. Given this criterion, the entry groups G7 of Set 1 and G6′ of Set 2 may be considered as best adapted to the target area, as they were among the highest yielding groups in the lowest yielding environments, while maintaining an above-average yield in all other environments as well.

CONCLUSIONS

The great hybrid superiority observed in the present study makes hybrid breeding of sorghum for the target semi-arid area in Kenya a promising approach. Our results are supported by the superiority of hybrids over local cultivars in East and West African environments found earlier (Doggett and Jowett, 1966; Kapran et al., 1997). However, one should be aware that hybrid production and successful marketing requires skilled labor, an effective seed industry, a good infrastructure, and a sufficient income for the farmers to be able to afford the costly hybrid seed. These prepositions are not ubiquitous. Instead of hybrids, other types of cultivars could be produced which capitalize on heterozygosity, e.g., synthetics built up from components with superior combining ability and high outcrossing rates. Although syn-

thetic cultivars may not have the same vigor as the hybrid blends evaluated in the present study, they have several advantages. A synthetic cultivar can be regrown for a few seasons without serious changes in its genetic composition, which is convenient for the small-scale farmers. If components are selected for specific adaptation to different types of drought stress, synthetic cultivars can also make use of populational buffering for increased yielding stability.

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Economic Efficiency of One Cycle of Marker-Assisted Selection

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ABSTRACT

The efficiency of molecular markers to improve genetic prediction has been proved by many studies. Nevertheless, the additional cost due to marker genotyping is seldom considered in the comparison between marker-assisted selection (MAS) and phenotypic selection. In the context of plant breeding, the relative cost efficiency of MAS in the first cycle of selection is evaluated through an analytical approach taking into account the effect of the experimental design (population size, number of trials, and replications per trial) on quantitative trait loci (QTL) detection. The same global cost is assumed for both methods. In a first step, the optimal allocation of the experimental resources is studied for each method before comparing them at their optimum. For traits sensitive to genotype × environment interactions, unreplicated trials are optimal for both methods but the optimal number of trials is different. It increases with the investment for phenotypic selection while it becomes nearly equal to one for MAS. The loss of efficiency due to non-optimal designs is evaluated. The expected economic return of MAS compared with phenotypic selection decreases with the cost of genotyping. When this cost is high, MAS interest is limited to traits with a low heritability, provided that the investment is high enough to evaluate a large population size, which is the necessary condition to explain with markers a large part of genetic variation. The maximal genotyping cost that is acceptable for MAS to be efficient is given for different values of investment and trait heritability.

F OR THE LAST DECADE, rapid progress has been made in molecular marker techniques. For many species, the number of polymorphic markers is now sufficient to build dense maps and to localize individual QTL. Once marker-QTL associations have been detected, they can be used to improve the prediction of genetic values. This use of markers in selection schemes has received extensive interest in the recent past. Lande and Thompson (1990) proposed to identify marker-QTL associations by multiple regression of phenotype on marker type and to select individuals on an index combining phenotype and molecular value predicted with markers. The efficiency of this method of marker-assisted selection (MAS) relative to purely phenotypic selection has been widely studied, mainly in the case of populations derived from the cross of two inbred lines, through analytical approaches (Lande and Thompson, 1990; Luo et al., 1997; Moreau et al., 1998) and simulations (Zhang and Smith, 1992, 1993; Gimelfarb and Lande, 1994, 1995; Whittaker et al., 1995, 1997; Hospital et al., 1997). All these theoretical studies concluded that in many situations, MAS could be more efficient than phenotypic selection.

Despite these promising results, to our knowledge, few MAS experiments have been conducted with the approach proposed by Lande and Thompson (1990). This is certainly partly due to the cost of MAS experiments, which require both phenotypic and molecular evaluation. In all the theoretical studies mentioned above, the problem of the additional cost due to marker evaluation is not taken into account. Both methods of selection are assumed to be conducted in the same agricultural conditions, that is to say, assuming equal population sizes and identical experimental designs. In this situation, the additional cost associated with the marker evaluation is ignored, which leads to overestimating the

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